Cueva Antón: a multi-proxy MIS 3 to MIS 5a palaeoenvironmental record for SE Iberia

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ABSTRACT

Overlying a palustrine deposit of unknown age (complex FP), and protected from weathering and erosion inside a large cave/rock-shelter cavity, the sedimentary fill of Cueva Antón, a Middle Paleolithic site in SE Spain, corresponds in most part (sub-complexes AS2-to-AS5) to a ca.3 m-thick Upper Pleistocene terrace of the River Mula. Coupled with the constraints derived from the deposit's paleoclimatic proxies, OSL dating places the accumulation of this terrace in MIS 5a, and radiocarbon dates from the overlying breccia *cum* alluvium (sub-complex AS1) fall in the middle part of MIS 3; the intervening hiatus relates to valley incision and attendant erosion. The two intervals represented remain

largely unknown in Iberia, where the archeology of the early-to-middle Upper Pleistocene is almost entirely derived from karst sites; Cueva Antón shows that this dearth of data, often interpreted in demographic terms, has depositional underpinnings ultimately determined by past climate variation. In early MIS 5a, the paleobotanical evidence indicates climate conditions similar to present, albeit wetter, followed by progressive cooling, reflected in the replacement of Aleppo pine by black pine and, at the very end, juniper-dominated landscapes — the latter characterizing also mid-MIS 3 times. The variation in sedimentary facies and composition of the mollusk assemblages reflects the changing position of the river channel relative to the back wall of the cave. Such changes represented the major constraint for the occupation of the site — most of the time inaccessible to terrestrial mammals, it was used throughout by the eagle-owl, explaining the abundance of rabbit bones. Human occupation occurred during a few, short windows of availability, and is reflected in well-preserved living floors defined by hearths, artefacts, and the remains of hunted herbivores. The stone tool assemblages are Middle Paleolithic, which, in Europe, implies a Neandertal identity for their makers and, hence, that Neandertals persisted in the region until GI 8. Cueva Antón's high-resolution record provides unique, critical information on the paleoenvironments and adaptations of humans in two short windows of time during which wetter conditions existed in SE Iberia, where arid or semi-arid climates prevailed through most of the Upper Pleistocene and the Holocene.

KEYWORDS

Marine Isotope Stage 5a; Greenland Interstadial 8; Luminescence dating; Radiocarbon dating; Aleppo pine; Middle Paleolithic; Neandertal

HIGHLIGHTS

- High-resolution continental record of environmental change
- Wetter conditions during MIS 5a in a nowadays semi-arid region of Europe
- Seasonal Middle Paleolithic camping in non-palimpsest contexts
- Persistence of Neandertals up to GI 8 in SE Spain

1. INTRODUCTION

Cueva Antón (Mula, Murcia, Spain; 38°03'52" N; 01°29'47" W) is a cave/rock-shelter site located on the right bank of the River Mula (Fig. 1). Nowadays, the reservoir created by the La Cierva dam, erected between 1915 and 1929, fills this stretch of the valley. Silting-up (by the 1980s, 24.5 m of deposits had already accumulated at the point of damming) made it necessary to raise the existing wall from 358 to 364 m asl (above sea level). This work, carried out between 1987 and 1996, partially restored (to 5 hm^3, at normal maximum level) the reservoir's original, 8 hm^3 capacity (Gómez-Espín et al., 2005).

As the mouth of Cueva Antón lies between 351 and 359 m asl, the site had been subject to long-term inundation ever since the dam gates were first closed but, at full storage, the enlarged lake created by the raising would completely submerge it. Consequently, excavation of a test trench was included among the mitigation measures arising out of the project's environmental impact assessment. This archeological investigation, carried out in 1991, opened two trenches: a 2 m×1 m (Zone II), which cut through post-dam deposits only, and a 3 m×3 m (Zone I), which yielded Middle Paleolithic occupation horizons at the base of a thick, well-stratified fluviatile sequence (Martínez-Sánchez, 1997) (Fig. 2). Based on

117 correlation with the valley's 5-7 m terrace and the latter's inferred chronology, the 1991
118 investigation dated the upper part of the sequence to ca.38-40 ka.
119 Interest in the site was revived in 2006 (Zilhão et al., 2010a, 2012; Angelucci et al., 2013;
120 Burow et al., 2015). During a first, week-long field season in August of that year, the Zone I
121 trench was emptied from a thick layer of debris resulting from the erosion of its exposed
122 walls, compounded by occasional flooding. This was followed, in 2007-08, by two month-
123 long summer field seasons. In 2009-10, however, a year-round reservoir high impeded
124 access to the site and inundated the excavation trench (Fig. 1). On this occasion the damage
125 was minimal, so investigations could resume, but, in the early autumn of 2012, a massive
126 flash-flood event, and the prolonged submersion of the site that followed, caused a major
127 collapse of trench walls and fieldwork had to be suspended.
128 Given Martínez-Sánchez et al.'s (1997) dating, Cueva Antón appeared to be a target of
129 choice for an investigation of the last stages of Iberia's Middle Paleolithic and the hypothesis
130 of late Neandertal persistence south of the Ebro drainage (Zilhão, 1993). In addition, the
131 nature of the sedimentary envelope warranted an expectation of high stratigraphic integrity
132 for both artefacts and ecofacts, making it possible that these twin issues be addressed with
133 assemblages and samples free of the thorny issues of definition and association
134 underpinning ongoing controversies (Zilhão, 2006; Zilhão and Pettitt, 2006; Finlayson et al.,
135 2008; Zilhão et al., 2010b; Kehl et al., 2013; Wood et al., 2013). Eventually, our investigation
136 of this archive showed that its sequence spanned some 50,000 years of the early and middle
137 parts of the Upper Pleistocene, provided significant archeological and paleoenvironmental
138 information on periods of MIS 5 and MIS 3 that were largely unknown in Iberia, and shed

139 light on how climate change impacted the environment and the adaptations of humans in
140 the nowadays semi-arid regions of the peninsula's Southeast.

141 **2. REGIONAL SETTING**

142 The drainage basin of the River Mula occupies an area of 660 km² where the mean
143 annual temperature is 19.7 °C and mean annual rainfall ranges between 350-500 mm,
144 upstream from the La Cierva dam, and 250-350 mm, in the badlands extending downstream
145 of the town of Mula. The dominant soil temperature regimes are thermic, and soil moisture
146 regimes are aridic to xeric (García-Cortés et al., 1999). The current vegetation is a xerophytic
147 brushwood with *Artemisia herba-alba*, *Rosmarinus officinalis* and *Stipa tenaccisima*; Aleppo
148 pine (*Pinus halepensis*) and juniper (*Juniperus phoenicea*, *J. oxicedrus*) thrive in areas with
149 deeper soils, while *Tamarix*, *Nerium oleander* and *Phragmites* occur along river margins.

150 The earliest rocks outcropping around the site are those of late Mesozoic age deposited
151 in the Mula-Pliego piggy-back basin (Martín-Martín and Martín-Algarra, 2002). Surface
152 morphologies are largely controlled by subsequent tectonic activity, which generated a
153 geologically and structurally complex setting. Two main groups of formations may be
154 distinguished. On one hand, we have Cretaceous to upper Miocene sedimentary rocks
155 intensely affected by the Alpine orogeny (mostly limestone and marl, with occasional
156 sandstone and conglomerate); these rocks belong to a small paleogeographic and structural
157 domain (the "Mula tectonic unit") and form a rather tight, NW-SE anticline partly covered by
158 post-orogenic sediments whose flanks exhibit overthrusts directed towards the fold's axis.
159 On the other hand, we have post-orogenic materials comprised of Upper Miocene
160 sedimentary (marl, conglomerate, limestone) and volcanic rocks, as well as Quaternary,
161 mainly slope and alluvial sediments (IGME, 1972a, 1972b) related to the activity of the River

Mula, whose basin began to form in the Early Pleistocene. Mather et al. (1995) identified six main terraces at relative heights of 65 m, 40 m, 32-36 m, 15 m, 5 m and 2 m, while our own surveys identified another at 20-22 m above the present riverbed. Except for the one at 32-36 m, all the terraces are typically fluvial, and their bulk is formed of classical fluvial sedimentary facies (floodplain, bar, channel).

Cueva Antón opens in one of the Mula basin's tectonic overthrusts: a several hundred meter-long, roughly NE-SW-oriented reverse fault escarpment modeled into Eocene limestone. In its exposed face, a number of bedrock types (namely, calcareous breccia and conglomerate, calcarenite, and micritic and nummulitic limestone) are apparent. Originally, this ridge formed the southern flank of the El Corcovado gorge's initial section, nowadays entirely submerged by the La Cierva reservoir. The original depth of the incision can be pictured from the ca.100 m difference in elevation between riverbed and adjacent terrain observed at the damming site; between this point and Cueva Antón, the River Mula bridged, over ca.1 km, a difference in elevation of ca.50 m (SI Fig. 1).

Along with the neighboring Rambla Perea, which harbors functionally similar Middle and Upper Paleolithic localities (Zilhão et al., 2010c), the El Corcovado gorge would have provided one of the shortest routes for game and humans moving between the lowlands of the Mula basin and the mid-elevation Cenozoic limestone plateau northward of the Sierra de Ricote ridge, where Paleolithic occupation is documented by cave art sites (Salmerón et al., 1999). Indeed, a number of Middle Paleolithic open air localities are known even farther North, near the border with the adjacent Mesetan lands of Albacete (Zilhão and Villaverde, 2008) (Fig. 1).

3. MATERIALS AND METHODS

The 2007-12 field work used the 1991 grid and datum. At the end of the 2012 season, four trenches had been opened (Fig. 2): East (Z-I/18-22), Central (J-L/16-19), West (N-Q/19-21) and Extension (M-O/18-19).

In 2007-08, the focus was on the upper part of the succession, where we encountered sparse, spatially and stratigraphically discrete evidence of human occupation. In archeologically fertile units, all stone tools, mid- and large-sized faunal remains and charcoals detected during excavation were piece-plotted, and all sediment was dry-sieved. In sterile layers, piece-plotting was limited (to e.g., charcoal, large bone fragments) and sandy units were dry-sieved; wet-sieving was used exceptionally for the acquisition of lagomorph and micromammal samples in silty-loamy units rich in such remains. Two-sieve stacks (2 and 1 mm mesh-sizes) were used throughout.

In 2011-12, the focus was on the basal, archeologically rich horizons. Cut-offs for piece-plotting were set at 2.5 cm for lithics (except when technologically relevant, e.g., retouched piece fragments, resharpening flakes), and 5 cm for faunal remains (except when identifiable to species or body part, e.g., epiphyseal fragments or teeth). Spatially, the different occupation surfaces were dealt with as a single unit; excavation proceeded via "peeling off" (*décapage*) along observed boundaries, whether natural (e.g., the interface with the underlying geological stratigraphy) or anthropogenic (e.g., the base of distinct occupation floors stacked up within a single natural stratigraphic unit). The sediment in fire features and in a 2.5 m-deep "telephone booth" (square I20; complemented, for the basal units, by two ½ m^2 trenches in K20 and L20; Fig. 3) was floated in its entirety; the rest was dry-sieved as before (in archeologically fertile units) or discarded (in sterile ones).

All *décapage* surfaces and cross-sections were recorded using digital photography. Photo mosaics were assembled using PT GUI© or Microsoft ICE© and orthorectified with the University of Venice's RDF© software. Elevation maps and 3D models were produced with Surfer©. The methodology implemented in the stratigraphical and micromorphological study of the site and the OSL dating of its sediments is laid out in Angelucci et al. (2013) and Burow et al. (2015), respectively. The charcoal samples used for radiocarbon dating were first identified to taxon and then ABA- or ABOx-processed following Brock et al. (2010). Pollen analysis was carried out in the archeobiology labs of the CSIC in Madrid and the EPOC lab of Bordeaux; neither sodium pyrophosphate nor acetolysis were used (Sánchez-Goñi et al., 1999; López-Sáez et al., 2003). Charcoal analysis followed Badal et al. (2012). The mollusk samples come from the "telephone booth," and include shell collected in all mesh sizes down to the smallest (0.5 mm); they were analyzed using standard protocols (e.g. Evans, 1972), where minimum totals are estimated from the number of apices or apical fragments for gastropods, or hinges in the case of bivalves.

The lagomorph samples studied here come from two squares excavated in 2007 and were analyzed following Sanchis (2012). The piece-plotted remains of large mammals, birds and tortoise were analyzed for surface modifications induced by geological processes and biological agents, and identified to the most precise taxonomic, anatomical and age-class level possible, using standard criteria (Mariezkurrena, 1983; Di Stefano, 1995; Lister, 1996; Sanz et al., 2014) and the reference collections of the Natural History Museum, Barcelona (MCNB-Cord), and the LARC laboratory, Lisbon; sieve finds were determined with similar precision whenever possible.

4. RESULTS

4.1. Stratigraphy

Using the West wall of the 1991 Zone I trench as reference (Fig. 4), and maintaining the terminology of Martínez-Sánchez (1997) for the designation of individual units, Angelucci et al. (2013) provide detailed description of the Cueva Antón sediments (Table 1). From top to bottom, the succession features four complexes:

- **DD (dam deposit).** Well-bedded fine sediment (mainly silt) accumulated by decantation on top of the Pleistocene sequence as a result of post-1929 episodes of long-term submersion by the La Cierva reservoir.
- **TL (transitional layers).** Heterogeneous units below the DD complex, resting on an erosive surface dipping outwards, formed of Pleistocene material reworked by post-1929 inundation episodes and of backfill from the 1991 excavations.
- **AS (archaeological succession).** Laterally variable fluviatile accumulation of Upper Pleistocene age featuring distinct sedimentary facies and intercalations of lenses of slope deposits generated by wall degradation processes; the presence of discontinuities allows the recognition of five main phases of deposition, differentiated as sub-complexes AS1 to AS5.
- **FP (fine palustrine).** Fine-grained, weakly bedded sediment of unknown age, rich in organic matter, containing vegetal pseudomorphs, some charcoal, and mollusk shell.

The lowermost complex corresponds to unit IV of the 1991 trench, then recognized in square L22 over a thickness of 65 cm, down to 351.5 m asl. Having since found bedrock at 352.5 m in squares L/16-18, 353 5 m in square I20, and 355.0 m in square B21, we infer that FP fills-up a narrow, deep fissure running along the back wall of the site.

252 The five sub-complexes differentiated within AS reflect the changing position of the river
253 channel relative to the back wall. During the accumulation of AS5 (layers II-u to III-n), the
254 Mula flowed outside and the cave's interior floor space was a sand beach formed by low-
255 energy flooding events; this phase ended with an episode of biostasis long enough for a
256 poorly developed alluvial paleosoil to form over a ground surface corresponding to the top
257 of unit II-u. AS4 (layer II-ø) reflects the resumption of sand beach/lateral bar formation
258 under similar conditions; this resumption was followed by migration of the channel towards
259 the external side of the meander and concomitant erosion of the deposit previously
260 accumulated inside the cave, resulting in the formation of a low levee (represented by the
261 surviving AS4 sediments) separating the channel from the wall. AS3 (layers II-n to II-t)
262 formed when the channel moved slightly outward, thereby leaving inside the cave a band of
263 temporarily inundated, boggy land, roughly corresponding to rows 18-22 of the grid;
264 eventually filled-up in clay-plug manner, this stretch of terrain transitioned to riverbank
265 conditions northward of row 17, as indicated by the dense, intricate interdigitation of silty-
266 loamy and sandy lenses observed there (Fig. 4). The channel then swung back to the
267 external part of the meander, with the stream now flowing directly against the back wall of
268 the cave, resulting in the formation of AS2 (layers II-d to II-m) — 50-70 cm of stratified
269 gravel, coarse sand, and sand bars accumulated on top of the previous phase's fine
270 sediments.
271 Longitudinally, the AS2-AS5 sequence dips W, probably as a result of bedrock
272 topography. Sagitally, stratigraphic interfaces are broadly horizontal, even though a slight
273 northward dip is apparent within AS5 and the boundary between AS2 and AS3 is basin-
274 shaped (SI Fig. 2). This pattern reflects accumulation above a minor embankment with no

275 significant back slope separating the site from the riverbed. Conversely, the significant angle
276 of slope (ca.20°) presented by the Pleistocene deposit to the North of row 19 (as best
277 observed in the East cross-section of the Central trench; Fig. 5) indicates the presence of an
278 erosional bank reflecting post-AS2 river incision (SI Fig. 2). The end of this phase is marked
279 by an episode of stabilization during which a thick calcareous crust formed: inward of row
280 19, as a largely uneroded layer II-d; outward, on top of the erosional slope's surface.
281 This pre-existing topography constrained the last Pleistocene phase of sediment
282 accumulation, represented by AS1, to a narrow band along the back wall (SI Figs. 2-3). As in
283 underlying units, the basal facies (layers I-i to II-b) are low-energy, water-laid. In the Zone I
284 and East trenches, a dense breccia of angular limestone debris (layers I-g, I-h and I-k) capped
285 this alluvium; its fine matrix may result from overbanking episodes and/or the
286 syndepositional progradation of sediments from the underlying sandy-silty facies coevally
287 exposed upslope.
288 Indicating the outline of the extant river margin, the breccia deposit capping AS1 wedged
289 out along column K and row 18 of the grid, while the basin shape of the interface with the
290 overlying DD complex implies erosional loss of the upper reaches of the original
291 accumulation (SI Figs. 2-3). Layers I-g, I-h and I-k are therefore to be understood as the basal
292 part of a truncated slope deposit that, in rows 20-21 of the grid, could have been some
293 50 cm thicker. In this case as much as in that of the surface of AS2 in the West trench, the
294 geometry of the erosive scar implies the action of water running along the back wall from
295 higher up and therefore originating in nowadays cluttered, upward-oriented passages that
296 once connected the cavity with the plateau above.

297 **4.2. Radiocarbon dating**

298 Initially, ten cut-marked or otherwise humanly-modified long bone shaft fragments from
299 layers II-t, III-f and III-j of the 1991 salvage work were selected for radiocarbon dating; five of
300 these, all *Cervus elaphus*, were analyzed and found to be completely collagen-depleted. A
301 second round of dating targeted well-provenanced charcoal samples. A first batch
302 underwent the standard ABA pre-treatment. The ABOx-SC approach was then applied to
303 assess whether incomplete decontamination might be making for results younger than the
304 samples' true ages.

305 In total, 51 samples from the following complexes or sub-complexes were submitted: 1
306 from DD, 1 from TL, 33 from AS1, 6 from AS2, and 10 from AS5. Of these, 22 were stored
307 away as reserves and 29 were analyzed. The success rates were 100% (three out of three)
308 for the ABA samples and 26% (five out of 19) for the ABOx samples. The low success rate of
309 ABOx is to be expected given the aggressiveness of the treatment and is in line with the
310 outcomes reported when applying the approach to contexts from broadly the same time
311 interval (Brock and Higham, 2009). The samples surviving the ABOx-SC pretreatment had a
312 high %C indicating that the material which survived was well preserved (Rebollo et al.,
313 2011).

314 Table 2 lists the results obtained for the successful samples. The statistically significant
315 difference of 1740±260 radiocarbon years between the ABA and ABOx-SC results for the
316 two sub-samples of J19-7 suggests that, in this site's specific geochemical setting, the ABA
317 pre-treatment is insufficient to achieve full decontamination. This is corroborated by the
318 likewise significant difference of 720±320 radiocarbon years between the ABA result for
319 layer I-k and the younger of the two indistinguishable ABOx-SC results obtained for this unit.

The amount of unremoved contamination implied by the difference between the ABA and ABOx results for sub-complex AS1 would suffice to bring the age of sub-complex AS2 from beyond the reach of radiocarbon dating to the interval indicated by the ABA result for layer II-h/i. Consequently, (a) the single radiocarbon date available for layer II-h/I should be treated as a minimum age for the deposition of AS2, and (b) only the ABOx-SC results should be retained to estimate the chronology of the AS1 deposit, which they restrict to the three millennia comprised between 37.7 and 34.6 ka.

4.3. Luminescence dating

Ten sediment samples were obtained from the East and West profiles of the Zone I trench in September of 2010 (CA-1 to CA-6) and 2012 (CA-9 to CA-12), of which nine could be dated; the different tests reported by Burow et al. (2015) indicate that all were well bleached. As the sampled units were texturally homogeneous and preserved evident cross-bedded lamination across their extensive excavated surfaces, the dispersion observed in paleodose measurements must reflect microdosimetry effects or experimental scatter rather than the presence of mixed grain populations; consequently, burial doses were estimated with the CAM (Central Age Model) model. The analytical data and results obtained are reproduced in SI Table 1.

Taking all estimates into account, Burow et al. (2015) calculated error-weighted mean ages for the different units and the sequence as a whole, following Jacobs et al. (2011, 2013) but using a more conservative systematic uncertainty of 5% instead of 2%. For the accumulation of sub-complexes AS2-to-AS5 as a whole, the error-weighted mean age thus obtained was 72.0±4.2 ka for an assumed water content of 5±3%. This result is consistent

342 with sedimentation taking place during (a) MIS (Marine Isotope Stage) 5, ceasing with the
343 onset of MIS 4, (b) late MIS 5 and early MIS 4, or (c) early MIS 4 only.
344 Because water has a higher radiation absorption coefficient than air, water content is a
345 critical parameter in the calculation of luminescence ages: overestimation may result in ages
346 that are too old, underestimation in ones that are too young. Burow et al. (2015) assumed
347 predominantly cold and dry climate conditions during the Late Pleistocene and, in line with
348 the assumption and considering the deposit's sheltering from direct precipitation, corrected
349 dose rates using the 5±3% average of all samples. The measured water content, however,
350 was higher for the 2010 samples (12.1±5.4) and lower (2.4±0.7) for the 2012 samples (Table
351 3). This discrepancy relates to the conditions at the time of sampling: the 2010 work was
352 carried out on September 21, four weeks after the reservoir had begun to descend from a
353 more than one year-long high; the 2012 work was carried out on September 6, after a more
354 than one year-long low during which it dried out in front of the site for extended periods of
355 time (SI Fig. 4). These oscillations are relevant because the rocky ledge separating the
356 shelter from the riverbed (Fig. 1B) is insufficient to isolate the fill from the effects of
357 capillarity whenever the reservoir rises above 351-353 m asl — as observed in 2007-12, such
358 a level entails extensive impregnation of the succession's basal sandy deposits.
359 The radiocarbon dating of sub-complex AS1 and the fluvial nature of some of its units
360 (e.g., layer II-a) imply that Cueva Antón was subject to permanent or regular inundation
361 until at least 35 ka. Consequently, even if we account for significantly drier climatic
362 conditions during MIS 4, the 2010 mean value represents a realistic estimate of the situation
363 pertaining through at least half of the time elapsed since the fluviatile sequence began to

364 accumulate, while the 2012 mean value reflects the site's hanging-above-the-riverbed
365 position resulting from LGM and/or Holocene valley incision.
366 In order to estimate the impact of this problem, Table 3 provides ages calculated with a
367 range of estimates bracketing the actual measurements. Even with as much as 20%
368 (unrealistic for sandy deposits), the increase in age would be insufficient to place the
369 sequence in the range of MIS 5e. With a value of 12±6%, the average for the 2010 samples
370 and, hence, the value inferred to be closest to the long-term water content of the deposit,
371 the error-weighted mean ages for layer II-e and for sub-complex AS5 as a whole are,
372 respectively, 76.0±5.8 ka (p=0.94) and 76.2±4.8 ka (p=0.98), while the age for intermediate
373 sub-complex AS4 is 88.2±8.9 ka.
374 As the ages for AS2 and AS4 provide a *terminus ante quem* for sub-complex AS5, using
375 the 12±6% water content estimate favored here and following Lisiecki and Raymo (2005)
376 constrains the accumulation of AS5 to having begun after the MIS 5c peak (96 ka) and
377 having ended during MIS 5a (85-71 ka). Further constraining this interval and assessing
378 whether the deposition of AS4, AS3 and AS2 extended into MIS 4 requires consideration of
379 the paleoenvironmental evidence presented below and is therefore an issue we come back
380 to in the Discussion and Conclusions section.
381 **4.4. Pollen analysis**
382 Three rounds of palynological analysis were carried out at Cueva Antón. A column of nine
383 samples, spanning AS3 and AS5, was obtained in 2007 from a freshly excavated section in
384 the SW corner of grid unit L19 and analyzed in the Madrid lab. A column of 79 samples,
385 spanning AS4 and AS5, was obtained in 2008 from the west wall of Zone I (square L21) and

386 analyzed for pollen in the Bordeaux lab, which, to control for contamination, also analyzed
387 an additional 35 samples obtained from freshly exposed walls in the East trench of 2011.
388 In the L19 column, the samples from layer II-t and the base of layer II-u were sterile. The
389 other seven yielded pollen grains/gram of sediment in the range of 7×10^3 and could be
390 analyzed (Fig. 6). The fertile units were silt and clay, while the sterile ones were sandy
391 and/or cemented. In the other columns, however, the samples from fine-textured deposits
392 were also sterile — with two exceptions, ones whose concentrations and pollen counts
393 were nevertheless too low and insufficient to draw meaningful conclusions. This outcome
394 suggests that pollen preservation at the site is also controlled by spatial factors, namely the
395 geometry of layer II-ñ, which wedges out along column J of the grid (Fig. 4) but, westward,
396 forms a ca.20 cm-thick, impermeable cap of marly sediments protecting the underlying
397 sequence from leaching.
398 Contamination of the L19 samples by modern pollen can be ruled out because acetolysis
399 was not performed. High values of Asteraceae (*Aster*-type, Cardueae, Cichorioideae) and
400 fern spores can be indicative of post-depositional alteration, but only if coinciding with low
401 pollen concentrations and high counts of undeterminable pollen (Carrión, 1992a; Carrión et
402 al., 1999). This is not the case at Cueva Antón; the diagram in Fig. 6 thus reflects — with the
403 biases inherent to the differential production, dispersal, and conservation of pollen grains —
404 the extant vegetation.
405 Even though discriminating pine species on the basis of pollen dimensional criteria is
406 fraught with uncertainty (Desprat et al., 2015), *P. pinaster* could be identified in layer II-ñ
407 following Carrión et al. (2000) and based on details of exine morphology derived from
408 experience with the analysis of modern samples from the Spanish Central System, where

409 the different pine species of Iberia co-exist (López-Sáez et al., 2013). The dominant pollen
410 type is *P. sylvestris/nigra*, which represents trees that, nowadays, grow in the higher
411 mountains of Iberia under supramediterranean or montane climatic conditions (mean
412 annual temperature of 8-13 °C and 4-8 °C, respectively, and 400-1000 mm of annual
413 rainfall). Given its consistently high frequency (>67% throughout), this pollen type indicates
414 the local and/or regional existence of montane pine forests.

415 Where the other taxa are concerned, the samples cluster according to stratigraphic
416 subdivisions. Layer II-ñ contrasts with layers II-p and II-u in the relative importance of
417 deciduous *Quercus* (6-8% in II-ñ) and Poaceae plus Chenopodiaceae (9-20% and 4-8%,
418 respectively, in II-p and II-u), and in that *Juniperus*-type and Liliaceae are absent in II-p and
419 II-u but present (1-1.4% and 1-2.3%, respectively) in II-ñ. Layers II-p and II-u differ in the
420 latter's values of *Pinus sylvestris/nigra* (higher, 83-84%) and deciduous *Quercus* (lower,
421 <1%). The *Ephedra fragilis*-type is only present in II-u (1-1.4%), *Olea* is only present in II-p
422 and II-ñ (1%), and Scrophulariaceae (0.5-1%), *Juglans* (0.5%) and trilete ferns (1-1.4%) are
423 only present in II-ñ.

424 **4.5. Wood charcoal**

425 SI Table 2 gives the stratigraphic distribution of the charcoal analyzed so far. Sorting of
426 the floatation samples is incomplete, and most fragments fall in the 1-2 mm size range,
427 requiring additional SEM (Scanning Electron Microscope) analysis to achieve identification
428 to species; these results are therefore to be considered provisional.

429 By Holocene or Late Glacial standards, preservation is generally poor. The tissues are
430 altered by microbial and fungal activity (Fig. 7A-B) and, in some levels, contain reddish
431 particles (Fig. 7C-D) that, under SEM, could be identified as nodules of iron oxide generated

by hydromorphic dynamics as the plant tissues were penetrated by water (Badal et al., 2012). Based on the distribution of resin ducts in the growth rings as seen in transversal section (Fig. 7E,G), and the type of bordered pits in the cross fields as seen in radial section (Fig. 7F,H), two types of pines could be distinguished. Using the ecological affinities of these types and other diagnostic taxa, and excluding those fragments whose current classification lacks the taxonomic precision required to support ecological inference (grouped under Varia), we can divide the assemblage into the following vegetation categories (Rivas-Martínez, 1987; Gómez-Manzaneque, 2005):

- **Cryophilous** (*Pinus nigra* and/or *P. sylvestris* and *Pinus* sp. cf. *sylvestris/nigra*). As in the region, nowadays, these taxa only grow above 1000-1200 m, their presence in the much lower elevation catchment of Cueva Antón is indicative of a colder climate.
- **Steppic** (*Juniperus* sp., *Artemisia* sp., *Ephedra* sp., Fabaceae, cf. *Erica*, cf. Lamiaceae). Based on wood anatomy alone, these taxa cannot be identified to species level and therefore cannot provide temperature constraints; but they are all very aridity-tolerant and thrive in areas of poor soils or with <300 mm of mean annual rainfall.
- **Thermophilous** (*Quercus* sp. evergreen, *Quercus* sp. deciduous, *Quercus* sp., *Pinus halepensis* and *Pinus* cf. *halepensis*). At the latitude of Murcia, these taxa are found from sea level up to 1000-1200 m. Their ecological optimum corresponds to areas with mean annual temperatures of 13-19 °C and 300-500 mm of mean annual rainfall.
- **Riverside** (*Salix/Populus*, *Prunus* sp., cf. *Prunus* and cf. *Equisetum*). These taxa need humid soils and/or occur along the margins of more or less permanent streams.

The stratigraphic variation in the relative proportion of these categories is illustrated in Fig. 8. The chi-square test indicates statistically distinct assemblages (p<0.001) regardless of

455 whether they are compared simultaneously or as stratigraphically successive pairs. The
456 distinction remains even if (a) to avoid expected values below 5, the least represented
457 categories are removed from the comparisons, or (b) to filter out potential anthropogenic
458 biases, the artefact-bearing units are removed from the totals.

459 The diversity and abundance of thermophilous taxa shows that AS5 is the warmest and,
460 given the significant representation of deciduous oaks and riverside taxa, also the most
461 humid phase — as best exemplified by layer III-i/j. Around Cueva Antón, depending on soils
462 and other factors, this layer's charcoal assemblage implies oak woodlands and open Aleppo
463 pine forests growing under climatic conditions similar to the present. The AS3 and AS2
464 spectra reflect a trend to colder and more arid conditions, manifested in the progressive
465 disappearance of thermophilous trees, initially in favor of cryophilous (AS3), and then of
466 steppe (AS2) taxa.

467 **4.6. Mollusks**

468 Shells of non-marine mollusks occur throughout the floatation column (SI Table 3). The
469 preservation was generally good but many specimens were represented by small fragments
470 and the frequency variation between stratigraphic units is enormous. In part this is related
471 to disparity in sample sizes, but it mostly results from depositional context and taphonomy.
472 For instance, the sample from layer I-k represents some 0.5 m^3 of sediment and yielded
473 1002 identified shells, while the samples from III-b to III-k/l combined represent about the
474 same volume but yielded only 129. Based on knowledge of their present-day ecology, the 34
475 molluscan taxa (21 terrestrial and 13 aquatic species) recovered can be assigned to different
476 groups, although the boundaries between each group are not always sharp. Their frequency
477 by depositional context is given in Table 4.

478 Land snails, which are best represented, include a mixture of xerophilous species of dry
479 open ground, such as *Jaminia quadridens*, *Truncatellina callicratis*, *Pupilla muscorum*, cf.
480 *Xerotricha* and related forms (e.g. other 'helicellines'), those that inhabit rocks and screes
481 (e.g. *Granopupa granum* and *Pyramidula* sp.), as well as those that live in wetter places
482 (*Vallonia pulchella*, *V. enniensis*, *Vertigo antivertigo*, *Zonitoides nitidus* and
483 *Oxyloma/Succinea*). This last group would apparently include *Orculella aragonica*, a taxon
484 recently recognized as an Iberian species distinct from *O. bulgarica*, with which it was
485 formerly confused (Arrébola et al., 2012). *O. aragonica* prefers hygrophilous habitats such as
486 small marshes, and moist and waterlogged habitats in permanent freshwater spring areas
487 associated with limestone, and is restricted to the most humid habitats in semi-arid areas
488 during the summer months (Garrido et al., 2005). The remaining group of land snails are
489 catholic species that can inhabit a broad range of different habitats. Species characteristic of
490 woodland or other strongly shaded habitats are absent from the sequence.
491 Aquatic taxa generally occur at lower frequencies, and are chiefly represented by species
492 of damp ground (e.g. *Galba truncatula*), or small water-bodies. Species of *Pisidium*
493 (especially *P. nitidum*) occur in most of the shell-bearing samples, together with hydrobiids
494 (cf. *Pseudamnicola/Mercuria*); other taxa, such as *Theodoxus*, *Melanopsis*, *Bithynia*, *Radix*,
495 *Stagnicola*, planorbids and *Acroloxus*, occur only sporadically. This assemblage is fairly
496 typical of aquatic habitats found in limestone regions of southern Europe.
497 Since the counts are generally low for much of the profile, the subtle faunal variations
498 observed between strata should be interpreted with caution. However, there is a suggestion
499 that in many layers of the AS5 sub-complex, the proportion of land snails consistently
500 exceeds that of the aquatics, hinting at prolonged periods of subaerial exposure. Within the

terrestrial assemblages, the occurrence of *Pomatias elegans* suggests a temperate climate, similar to that of the region today, during the formation of AS5 (restricted to layers III-e/h and III-k/l, this climatically sensitive species is intolerant of prolonged winter cold; Kerney, 1968). The catholic species *Trochulus* cf. *hispidus* outnumbers the drier, more open-ground 'helicellines' in layer I-k, but this is not the case in much of the earlier part of the sequence; as this layer is also rich in hygrophilous species (e.g. *Orculella aragonica*), more humid conditions would seem to have existed in AS1.

The FP sample is unique in being dominated by *Granopupa granum*, a small chondrinid land snail that inhabits dry open calcareous places, including grassland, rocks and screes (Gittenberger, 1984); other xerophilous species (cf. *Xerotricha* and *Vallonia costata*) are also present. None of these taxa would have lived in a marsh, the habitat inferred from the sedimentology; their association with *Zonitoides nitidus*, which does inhabit marshland, and *Melanopsis,* an inhabitant of hard substrates in clean fresh water, indicates a taphonomically mixed assemblage implying complex depositional processes.

4.7. Lagomorphs

Initially (2006-07 field seasons), lagomorph remains were systematically collected, but we quickly realized they were likely to reflect natural accumulation processes. To test this hypothesis, two 2007 samples were submitted to in-depth analysis: one, obtained from dry-sieving, combined layers II-k and II-l of grid unit N20; the other, acquired in grid unit L16 via deflocculant-aided wet-sieving, came from layer II-u (SI Table 4). The results reported here concern these two samples.

All bones are of rabbit (*Oryctolagus cuniculus*), and most (98.9% in II-k/II-l; 96% in II-u) could be determined to skeletal part. The mortality profiles (Fig. 9) suggest age-selection, as

524 adults >9 months-old are the best represented class in both samples. A few individuals
525 (MNI=10 across both samples) are about one month-old but bear the same taphonomic
526 marks as older juveniles and adults; they reflect predation of young rabbits when first
527 venturing out of the warren, a phase during which they are highly vulnerable.
528 Skull and limbs dominate skeletal part representation (Fig. 9). The subtle differences
529 between the two samples correlate well with visibility-at-sorting under field conditions: the
530 dry, sandy II-k/II-l sediments allowed for easy recognition of even the smallest elements of
531 the skeleton, whose retrieval was made an arduous task by the loamy matrix of layer II-u.
532 This factor probably explains as well the lower representation of young and very young
533 individuals in II-u (only 10% of the MNI, contra 30% in II-k/II-l).
534 Breakage patterns (SI Tables 5-6), namely the short length of long bone fragments and
535 the green bone nature of the fractures, which tend to be found in association with
536 modifications caused by the beaks and claws of large birds of prey, are characteristic of the
537 damage inflicted on the skeleton as raptors break the rabbit into fragments of a size they
538 can ingest (Lloveras et al., 2009; Sanchis, 2012). Indeed, ca.12% of the bones analyzed in
539 each layer carry diagnostic evidence — predominantly moderate or light (47.6% and 36.8%,
540 respectively, in II-k/II-l, the corresponding values for II-u being 60.8% and 34.7%) — of the
541 action of digestive acids, which mostly affects porous articulations and limb apophyses (and,
542 in II-u, the axial skeleton as well) (Fig. 10).
543 Even though the bones of small birds, common among the microfauna, remain
544 unstudied, the larger specimens retrieved in layers I-k and II-u corroborate these inferences.
545 The distal humerus from layer I-k (SI Fig. 5) belongs to an Anatidae. The remains from layer
546 II-u (SI Table 7; SI Fig. 6) correspond to a cluster of eagle-owl (*Bubo bubo*) limb bones found

close together (some appeared to still be in semi-anatomical connection). These bones probably represent deaths-in-the-nest and identify the raptor responsible for the site's lagomorph accumulations. The beak- or claw-inflicted notch and punctures apparent in the duck humerus indicate that its presence in artefact-yielding layer I-k reflects not human predation but environmental background noise — i.e., eagle-owl preying, as with that layer's abundant rabbit bone component.

A ledge running high above the fill along the back wall of the cave would have provided optimal nesting space, and use of Cueva Antón by flying animals would have been possible even when the site's interior, emersed volume was otherwise inaccessible. Indeed, while excavating stratigraphic units accumulated by decantation we often observed the presence of intact pellets suggestive of single regurgitation events that must have been dropped by raptors perched directly above water (SI Fig. 7).

4.8. Larger mammals and tortoise

Data on the large mammal and tortoise remains from the 2007-12 excavations are provided in Table 5 and SI Tables 8-12 (the fauna from the 1991 work is a much smaller assemblage, largely composed of shaft fragments, and has not been studied yet). Ninety per cent of the specimens were recovered in layer III-b/d and in three different lenses, here collapsed into a single analytical unit, of layer III-i/j. Non-identifiable fragments were classified according to shape — flat, long or spongy — and body size— small (roe deer and ibex), medium (red deer) and large (large bovids, horse, rhino). Based on dental development stage and degree of wear, loose teeth and dentitions were assigned to five age groups: foetal/neonatal, infantile (milk teeth in use), juvenile (deciduous dentition in replacement), adult (permanent teeth) and senile (advanced occlusal tooth wear). As the

570 diagnostic features present on long bone shafts (e.g. foramens, grooves) allow the
571 recognition of small fragments, some bones (e.g. deer metapodials) are comparatively over-
572 represented.

573 Cervids are the most abundant taxon and, reflecting this abundance, “medium” is the
574 predominant ungulate size class. Assignment to species is complicated by fragmentation and
575 the coexistence of *Cervus elaphus*, *Dama dama* and *Haploidoceros mediterraneus* in the
576 MIS 5 of Iberia. Following Lister (1996), a well-preserved scapula from III-b/d (Fig. 11, no. 14)
577 featuring a mild flattening of the edge and a rounded and elongated profile of the glenoid
578 fossa would be fallow deer. Di Stefano (1995), however, has argued that these features are
579 insufficient to exclude red deer.

580 Given the absence of antlers and the non-diagnostic nature of the postcranial parts
581 retrieved, the presence of *Dama* and/or *Haploidoceros* can be neither demonstrated nor
582 rejected. The presence of red deer, however, is certain, as shown by:

583 • The existence of a few upper canines; following d’Errico and Vanhaeren (2002), a right
584 upper canine from III-i/j would have belonged to a <10 year-old stag, while an upper
585 canine from III-b/d would have belonged to a senile female.

586 • The absence of a step between the second and third lobes of the lower third molars (e.g.
587 Fig. 11, no. 5) (Di Stefano, 1995; Lister, 1996).

588 • The strong expression of (a) the lingual columns and the in-between furrows of the lower
589 molars, and (b) the buccal cones and stylids of the upper molars (Lister, 1996).

590 Deer are followed in abundance by horse, ibex, and tortoise. Roe deer and rhino are
591 scarce. Rhino is documented in III-i/j by deciduous teeth reflecting a maximum age at death
592 of 1.5 years. The morphology and size of the premolars (Fig. 11, nos. 1-2) is consistent with

593 *Stephanorhinus hemitoechus* (Guérin, 1981) and excludes appurtenance to *Coelodonta.*
594 Tortoise (*Testudo hermanni*) remains (Fig. 11, nos. 7-8) were found in III-b/d and III-i/j, and
595 mostly correspond to carapace plates, although there are also a few postcranial bones and
596 plastron remains. No fresh-water turtles were identified. Carnivores are represented by
597 non-hyena coprolites (in I-k) and an isolated lower premolar of bear (in III-i/j). The
598 preliminary field identification of *Castor fiber* in unit II-p/q/t (Angelucci et al., 2013) is
599 unconfirmed; the suspected specimen (Fig. 11, no. 9) is a horse tooth fragment.
600 Gnawing damage is anecdotical, and there are no digested bones. In contrast,
601 anthropogenic marks (Tables 13-15; Fig. 12 and SI Fig. 8) are ubiquitous, and especially so in
602 the units where human occupation is documented by stone tools and fire features, namely
603 I-k, III-b/d and III-i/j. Based on the anatomical parts represented and the position of the cut
604 marks, skinning, defleshing, evisceration, and carcass disarticulation are the activities
605 represented. Combined with the green-bone morphology of the breaks, the presence of
606 percussion scars shows that the assemblage's high degree of fragmentation (SI Table 10)
607 results from deliberate human action, namely for marrow extraction — especially well-
608 apparent in the longitudinal splitting of deer phalanges (SI Fig. 8, nos. 4, 8).
609 A few rounded bones (some to a high degree, entailing loss of surface morphology) have
610 been found in II-l and II-m, suggesting an alluvial origin for these small assemblages. Natural
611 processes may also explain the wholly uncharacteristic (e.g., complete or articulated)
612 remains retrieved in II-p/q/t and II-u (where artefacts are absent or represented by isolated,
613 probably transported finds): in the former, a complete deer metapodial; in the latter, the
614 articulated foot (phalanxes and sesamoids, all specimens complete) of a juvenile deer.

615 The 15 foetal/neonate bones in III-b/d and III-i/j could be reflecting predation focused on
616 females and fawns; even though the high degree of breakage prevents sexing of the
617 remains, this observation indicates that at least five females of either ibex or deer are
618 represented in the collection (three in III-b/d and two in III-i-/j). The erupting milk dentition
619 in a deer mandible from III-b/d (Fig. 11, no. 4) indicates an age-at-death of less than two
620 months — i.e., based on a May date-of-birth derived from extant southern Iberian
621 populations of red deer (Azorit, 2011), a summer kill. Likewise, a springtime kill can be
622 suggested for a foetal bone from the same unit whose large size indicates a near-term
623 mother. The other foetal/neonatal remains indicate winter-to-spring hunts.
624 Climate-wise, the absence of *Equus hydruntinus*, which, in Mediterranean Spain, is
625 typically associated with cold and arid conditions, and the presence of roe deer and tortoise,
626 substantiate the temperate nature of the assemblage. The tortoise is especially significant,
627 as it requires a mild climate with sunny and warm summers, without extreme temperatures,
628 and, critically for egg-laying, a soil temperature in the range of 22-35 °C (Hervet, 2000;
629 Nabais, 2010).
630 **4.9. Archeology**
631 Even though Martínez-Sánchez (1997) reports artefacts throughout AS5, the distribution
632 of the piece-plotted ones (Fig. 13) reveals full consistency between her data and the two
633 main units of occupation we were able to define in that sub-complex, III-b/d and III-i/j. The
634 apparent discrepancy reflects Martínez-Sánchez's (1997) treatment of facies representing
635 lateral variation within a single layer as if they were stratigraphically distinct units. Above
636 and below those lenses, the AS5 sands contained no more than a handful of isolated,
637 scattered artefacts (Table 6). Those retrieved in undisturbed, laminated sand units (e.g.,

638 layer III-e/h) must have been displaced from upstream by fluvial activity. Given the
639 characteristics of the associated fauna, that may also apply to the sidescraper and the two
640 flakes (plus the odd element of chippage) recovered in layer II-u.

641 Layer III-i/j is formed of three stratigraphically and spatially discrete concentrations of
642 stone tools and faunal remains associated with fire features. At the top, sub-layer III-i/j1
643 preserved actual hearths featuring thin horizontal layers of white ash above basin-shaped
644 accumulations of black sediments with an outer rim of reddish, thermoaltered sands (Fig.
645 14). That the ash was not scattered or washed away and the bones left behind were not
646 scavenged by carnivores suggests low-energy re-inundation of the site, with attendant
647 burial of the remains, soon after these hearths were in use. In the case of Hearth 5,
648 however, the partial erosion of the ash layer and the presence of injection features indicate
649 that turbation below the water surface affected the inundated ground floor to some extent
650 (Fig. 14). Less pristine preservation, resulting in the loss of the ash layer and of internal
651 microstratigraphic patterning, suggesting burial by somewhat higher energy flooding,
652 characterizes the other fire features so far documented in both III-i/j and III-b/d.

653 The sub-circular ash lenses and associated charcoal scatters of III-i/j1 correspond to fires
654 lit on a bare ground. The black and red staining of the underlying deposit reflects the
655 subsurface burning of organic matter and heat convection, not the prior excavation of a
656 *cuvette* — as shown by the fact that the color-altered sands preserve their original,
657 laminated structure. We can also tell that Hearths 5 and 4 were lit at different times
658 because of a stratigraphically intervening inundation event, well apparent in cross-section
659 view (Fig. 14). This observation illustrates how even such sub-layers as III-i/j1, the thinnest

660 units that the resolution of excavation tools allowed us to differentiate at the time of
661 digging, may actually subsume more than one episode of human occupation.
662 Bar a limestone chip from II-q/t, no artefacts were found in AS4 and AS3, and layer II-l is
663 the only artefact-yielding unit of AS2 — in total, 30 flint and limestone tools, cores and
664 flakes, plus some chippage. As the II-l deposit displays evidence of trampling (Angelucci et
665 al., 2013) and, therefore, of having remained emersed for a significant period of time, this
666 assemblage may stand for actual use of the place by humans. Its small size and lack of
667 association with anthropically modified animal bone suggests sporadic pass-through events,
668 not camping.
669 The artefact assemblage recovered in layer I-k was even smaller (Zilhão et al., 2010a). In
670 this case, however, the artefacts are associated with percussion-fractured animal bones and
671 abundant charcoal. Therefore, the low-number/low-density nature of the remains, coupled
672 with the absence of fire features, probably reflect spatial constraints (the narrowness of the
673 band of dry land then available for settlement inside the cave) combined with the operation
674 of syn- and post-depositional processes (colluvial dynamics of sediment accumulation, long-
675 term surface exposure of the finds, erosional truncation of the deposit).
676 Throughout, the stone tools are of Middle Paleolithic technology. Fig. 15 illustrates a core
677 and two sidescrapers from AS5, but the lithic assemblage recovered in layers II-l and I-k is of
678 a similar nature (Zilhão et al., 2010a). Despite its late chronology, I-k yielded no Upper
679 Paleolithic diagnostics. Its lithic assemblage is entirely made up of elements typical of, or
680 consistent with the Mousterian technocomplex, which, in Europe, is exclusively associated
681 with the Neandertals.

5. DISCUSSION AND CONCLUSIONS

5.1. Site formation and chronostratigraphy

A working hypothesis for the genesis and evolution of Cueva Antón is proposed in SI Fig. 9. The topographic cross-sections indicate that the cavity formed at the expense of a long, vertical joint controlled by local tectonics. Bearing in mind the abundance of bones in the overlying fluviatile succession, the fact that complex FP yielded none suggests accumulation in an endokarst setting, whereas its vegetable matter and mollusk remains indicate that the aquifer at the bottom of which the deposit accumulated was communicated with and formed part of a larger palustrine context then occupying the valley of the Mula outside. The elevation of the deposit relative to the valley's series of fluviatile terraces and the *terminus ante quem* represented by the dates for the overlying sequence imply that FP most likely accumulated during early MIS 5 times, but a late Middle Pleistocene age cannot be excluded.

Given the site's position in the external side of the vertex of a tight meander, undercutting by the stream (clearly at work during the last, Holocene phase of valley incision, as apparent in Fig. 1B), coupled with lateral erosion, must underpin the eventual breaking-open of the curtain of rock originally separating the joint from the river. As the cave opened, the fluviatile sediment making-up most of the AS complex concomitantly began to accumulate inside. The nodules of iron oxide generated by hydromorphic dynamics ubiquitously present in the charcoal found in the AS sediments, and the ecological affinities of the mollusk assemblages it yielded suggest that soil humidity remained high throughout. These proxies therefore provide additional support for the conclusion that the 12% water

content OSL results, based on the actual measurements associated with the 2010 sampling season, are our best estimate of the age of the AS2-to-AS5 sequence.

Under these dating premises, the *terminus ante quem* represented by the result for layer II-ø (88.2±8.9 ka), which implies a minimum age of 70.4 ka, places the deposition of AS4 and AS5 in MIS 5a, and the error-weighted mean age of 76.0±5.8 ka calculated for layer II-e, which implies a minimum age of 64.4 ka, excludes that AS2 and AS3 formed during MIS 3 (Table 3). Within these constraints, further resolution can be achieved via consideration of the chronological significance acquired by the site's paleoclimatic proxies when set against global records, namely the palynology of deep sea sediments (Sánchez-Goñi et al., 2008, 2013) and the sequence of interstadials (GIs) and stadials (GSs) derived from the variation in oxygen isotope ratios detected in Greenland ice cores (Rasmussen et al., 2014). Using the episode of paleosoil formation (layer II-u) documented at the top of AS5 as an anchor point for the correlations, the OSL dates allow us to contemplate three alternative models (A, B and C; Fig. 16).

If II-u is correlated with GI 19 or GI 20, then AS2 and AS3 would be of MIS 4 age (Model A), or such would possibly be the case with at least part of AS2 (Model B). Both hypotheses, however, are inconsistent with the paleobotanical evidence. Indeed, AS1 dates to GI 8, which is the most temperate interval of MIS 3; for instance, core MD952043, in the Alboran Sea, shows MIS 3 maxima of Mediterranean forest and of Mediterranean trees and shrubs at exactly this time (Sánchez-Goñi et al., 2009), when other pollen records also feature tree values of up to 40% at European sites below 40°N (Fletcher et al., 2010). Yet, the steppe signal in the Cueva Antón charcoal assemblage is significantly stronger in AS1 than in AS2 or

726 AS3, while the high percentage of tree pollen in AS3 indicates forested landscapes at local
727 and regional level (Fig. 8).
728 In addition, at the La Boja rock-shelter, located nearby in Rambla Perea, the abundant
729 charcoal found in LGM (Last Glacial Maximum) layers features 100% steppic spectra distinct
730 from any of those from Cueva Antón (chi-square test; p<0.001); for instance, in the Lower
731 Solutrean (ca.25 ka), *Juniperus* sp. are 97%, the remainder belonging to *Ephedra* sp. and
732 Fabaceae (Badal et al., 2012; N=298). Knowing also that the biogeochemistry of the Padul
733 lake record, in Granada, shows LGM-like aridity ca.66 ka, during MIS 4 (Ortiz et al., 2010),
734 and that the palynology of Alboran Sea core ODP976 (Masson-Delmotte et al., 2005) is in
735 tune with the pollen curve in Fig. 16 (derived from Atlantic core MD952042), we should
736 expect the charcoal in AS2 and AS3 to reflect the same extreme aridity seen in the LGM of
737 La Boja if these sub-complexes were of MIS 4 age; however, it does not. Consequently, AS2
738 and AS3 must have formed under conditions of less aridity than obtained at any time during
739 MIS 4 or even MIS 3. Based on the paleobotanical data thus far available we are therefore
740 led to conclude that the formation of the AS5-to-AS2 sequence took place entirely within
741 MIS 5 and reject Model A.
742 Correlating II-u with GI 20 (Model B) is also problematic. If a paleosoil had formed at that
743 time, we would expect paleosoil formation of similar or greater magnitude to have occurred
744 further down in the AS5 sequence if GI 21, which was three times longer (it lasted 7300
745 years, whereas GI 20 lasted 2300 and GI 19 lasted 1900), were represented in the deposit.
746 Since no such formation can be observed and no erosional hiatus capable of explaining the
747 absence exists below II-u, Model B implies that the underlying sediments would have
748 accumulated during the 1300 year-long GS 21 stadial. This implication, however, is at odds

749 with the temperate signal provided by (a) the *P. halepensis*-dominated charcoal
750 assemblages seen in layers III-b/d and III-i/j (SI Table 2), which also contain tortoise (Table
751 5), and (b) the presence of the *Pomatias elegans* snail in layers III-e/h and III-k/l (SI Table 3).
752 In Model C, the accumulation of AS5 and eventual soil weathering of its upper reaches
753 occurred during GI 21 and under climatic conditions broadly similar to present. Whether AS5
754 represented only the end of this interstadial or all of it would remain to be established, as
755 we currently lack a *terminus post quem* for the AS complex, but accommodating the
756 overlying AS4-to-AS2 sequence in the remaining portion of MIS 5a would be unproblematic.
757 Indeed, the persistence of oaks into AS3, the replacement of *P. halepensis* by
758 *P. sylvestris/nigra* in both AS3 and AS2, and the dominance of the latter over *Juniperus* sp. in
759 AS2 document a cooling trend matching that seen in global records between the onset of
760 GS 21, ca.77.8 ka, and the establishment of full glacial conditions in GS 19, at the onset of
761 MIS 4, ca.70.4 ka (Fig. 16). With current evidence, therefore, Model C best fits the
762 chronological implications derived from combining the site's OSL dating results with the
763 paleoenvironmental proxies they are associated with.
764 The episode of valley incision responsible for the erosive truncation of AS2 represents
765 change in the longitudinal profile of the River Mula, possibly related in part to global glacio-
766 eustatic processes, namely the lowering of sea levels during MIS 4. The stabilization and
767 incrustation of the talus slope formed as part of the river incision process must relate in turn
768 to the extended intervals of climatic amelioration apparent in the Greenland ice core
769 sequences after 50 ka, the last of which is GI 8, between 38.2 and 36.6 ka (Wolff et al.,
770 2010). Within this interstadial, a trend towards colder conditions is already apparent in
771 global records after 37.5 ka, and may well be reflected in the cryoclastic breccia making-up

772 the bulk of layers I-g, I-h and I-k — whose accumulation during the second, cooler half of
773 GI 8 is indeed consistent with radiocarbon dating results (Table 2). A new round of valley
774 incision eventually left the Cueva Antón succession hanging high above the riverbed,
775 explaining its excellent preservation — protected from slope dynamics and soil formation
776 processes by its position inside the site's large overhang, the deposit thusly became
777 sheltered from fluvial dynamics as well.

778 **5.2. Human occupation: constraints and characteristics**

779 During the time span covered by the AS complex, human occupation occurred in sporadic
780 and intermittent manner, as indicated by: (a) the complete absence of archeological
781 remains in most stratigraphic units; (b) the overall low number of finds made in those that
782 do contain some; and, (c) the ubiquitous presence of massive amounts of rabbit bones
783 accumulated by the eagle-owl (Table 6 and SI Table 4). As the long-term use of the site by
784 such nocturnal birds of prey is incompatible with it being within the reach of predators, we
785 can infer that, most of the time, Cueva Antón would have been separated from the
786 surrounding terrain by water or by extensions of boggy terrain unattractive to terrestrial-
787 based animals. This circumstance explains why burrowing by rabbit, badger, fox or lynx, the
788 bane of southern and western Iberian cave and rock-shelter archeology, is so conspicuously
789 absent from the sequence, and the more so if we bear in mind the size (73 m^2; Fig. 2) of the
790 excavated area. The single exception is the large chamber apparent in the East cross-section
791 of the Zone I trench of 1991 (SI Fig. 3). Our excavation of the I20 "telephone booth" and
792 adjacent squares showed that this burrow opened from the interface between AS1 and AS2,
793 i.e., that it probably formed during MIS 4, when no sedimentation would seem to have

794 taken place and, due to increased aridity, the site (as well as, most of the time, the riverbed
795 in front of it) would have been dryland.
796 The in situ archeology present in the basal river-accumulated sands implies periods of
797 sub-aerial exposure sufficiently long for the cave floor to be used for human settlement but
798 short enough for carnivores not to scavenge the abandoned animal bones, for rabbits not to
799 turn the site into a warren, and for fire features not to be eroded away — the implication
800 being that low-energy inundation quickly buried the remains left on the ground during the
801 visits permitted by such windows of availability. In such a scenario, a pattern of short-term
802 stays generating a quantitatively scarce but qualitatively rich archeological record is to be
803 expected. The artefact and ecofact contents of layers III-b/d and III-i/j meet this expectation,
804 as does their near-pristine preservation of features and minimal palimpsest effects. In
805 contrast, the ephemeral visits recorded in AS2 and AS1 reflect the significant reduction of
806 the space available for settlement as a result of migration of the channel toward the back
807 wall of the cave and post-MIS 5 valley incision.
808 The low numbers of rabbit in the anthropogenic bone assemblages from layers III-b/d
809 and III-i/j are consistent with these inferences: for instance, the 1 m² whence the 2007 II-
810 k/II-l sample came yielded a rabbit MNI of 90, while the 2 m² of III-b/d excavated the same
811 year with identical sieving and recovery criteria yielded a rabbit MNI of 1. On one hand, such
812 low amounts corroborate the natural origin of the abundant rabbit accumulations found
813 elsewhere in the sequence. On the other hand, they suggest that, at times when the site
814 could be and indeed was used by humans, the few remains of rabbit entering the
815 sedimentary fill stand for very short periods of eagle-owl nesting permitted by intermittent
816 flooding, if not simply for general environmental background noise.

817 The similarity in fire features, stone tool-kit composition (on-site knapping of locally
818 available limestone cobbles; flint represented by imported tools and resharpening debris)
819 and carcass-processing tasks (skinning, defleshing, evisceration, disarticulation) suggests
820 that human occupation episodes were functionally identical. The seasonality data available
821 for the archeological units in AS5 indicate use of the site between late winter and summer,
822 which is consistent with a cyclical pattern of flooding in autumn and early winter, followed
823 by dry season, spring-summer camping over the sand beach exposed once the water level
824 receded.

825 **5.3. Reconstruction of local paleoenvironments**

826 The high-resolution of the record enables detailed reconstruction of the site's immediate
827 environmental context. During MIS 5a, Cueva Antón opened directly onto the floodplain of a
828 permanently flowing River Mula. This is indicated by the characteristics of the sedimentary
829 succession, the presence of willow and/or poplar charcoal (hinting at a not too distant
830 riparian woodland, probably in the stretch of the valley extending upstream from the El
831 Corcovado gorge), and the preponderance of aquatic and marshland taxa in the molluscan
832 assemblages. The latter's dry and scree species, in turn, would reflect the habitats provided
833 by rocky ground inside and outside the cave, while the absence of species typical of strongly
834 shaded habitats is to be expected and does not exclude that the trees supplying the fuel
835 collected by humans around the site formed landscapes akin to today's Iberian pine forests
836 — with a well-lit floor and limited undergrowth (perhaps mostly consisting of juniper,
837 present throughout).

838 Taken together, the pollen and charcoal data might lead one to conclude that local
839 MIS 5a pine groves featured a mix of cryophilous and non-cryophilous taxa. However,

840 pending clarification of the environmental signal of layer II-u (where *P. sylvestris/nigra*
841 dominates the pollen spectra but >75% of the charcoal is *Pinus* sp. awaiting SEM analysis for
842 higher taxonomic precision), the representation of cryophilous pines in AS5 is marginal
843 (Table 4). Conversely, no *P. pinaster* charcoal has been identified in AS3, even though the
844 taxon is represented in the layer II-ñ pollen spectra. These mismatches indicate that the
845 local vegetation cannot be reconstructed as a patchwork of plant communities that,
846 nowadays, feature distinct ecological requirements. Rather, the Cueva Antón MIS 5a archive
847 most likely records an increasing colder climate, manifested in the passing through of the
848 boundaries between different altitudinal zones as they descended towards sea level.
849 Indeed, in Sierra de Espuña, which rises to 1583 m asl and is located <25 km SSE of Cueva
850 Antón, open stands of *P. nigra* with a juniper undergrowth exist above 1300 m, dense
851 *P. pinaster* groves with an undergrowth of deciduous trees and shrubs are found between
852 800 and 1400 m asl, and *P. halepensis* forests with an evergreen undergrowth occupy the
853 basal slopes, up to 800-1200 m asl (Sánchez-Gómez et al., 2003). Given the presence of
854 deciduous oaks in AS5 and AS3, and the absence of *P. halepensis* above layer III-b, a working
855 hypothesis for the pattern of change seen in the Cueva Antón sequence is that it reflects
856 how its location changed through time relative to the position of vegetation belts: within a
857 *P. halepensis* belt through most of AS5, at the interface between *P. pinaster* and *P. nigra*
858 belts through AS3, and within a *P. nigra* belt through AS2 and AS1.
859 In this scenario, the residual presence of *P. sylvestris/nigra* charcoal in the archeologically
860 fertile units of AS5 might result from the extensiveness of the inhabitant's economic
861 territory. If the latter covered several ecological zones, wood collected at significant
862 distance, either for fuel or as raw-material, could have entered the site, or such charcoal

863 could reflect the discard of wooden implements brought from elsewhere. The presence of
864 cryophilous pines in the charcoal of archeologically sterile layer III-k/l is in apparent
865 contradiction with this interpretation. However, due to the dip of the bedrock and the
866 rhythm of accumulation of the sediments, stratigraphically deeper human occupations have
867 been found within AS5 as our trench moved westward; consequently, the significant
868 amounts of charcoal recovered in III-k/l may simply reflect an as-yet unexplored occupation
869 horizon. Alternatively, the cryophilous pines found above III-b/d and below III-i/j could
870 represent the colder oscillations found within the overall warm/temperate conditions
871 pertaining through most of GI 21 that are apparent in both the Greenland ice and the deep
872 sea pollen records (Fig. 16).

873 More work needs to be done to address these areas of uncertainty, but the species
874 composition of the hunted fauna is consistent with an ecologically wide and geographically
875 large site catchment. Red deer and horse are mixed feeders with a preference for light
876 forests and grassland (García et al., 2009), while the diet of *Stephanorhinus* is thought to
877 mostly come from the kinds of herbaceous plants and scrubs that would have been
878 abundant in the floodplain and the open forests of surrounding slopes. Ibex, however,
879 requires rocky, steep, largely denuded terrain. Today, such terrain is only found at higher
880 elevation; indeed, the nearest known ibex herd lives in the Almorchón peak (which rises to
881 782 m asl), 15 km to the north of Cueva Antón (but we have sighted isolated individuals in
882 the nearby Rambla Perea; SI Fig. 10).

883 During mid-MIS 3, the charcoal data suggest an environmental setting similar to that
884 found at the very end of MIS 5a. By contrast with the earlier condition of a river channel
885 frequently changing its position relative to the back wall of the cave, the significant decrease

886 in the weight of dryland and scree mollusks (p<0.01 for a chi-square test of AS1 versus AS2-
887 AS5 combined) is consistent with the permanent, immediate proximity to the riverside
888 inferred from the geometry of the deposit.

889 **6. CONCLUDING SUMMARY**

890 By comparison with the present time, the broader implications of the Cueva Antón
891 record for the now semi-arid regions of SE Spain would seem to be the following:

892 • At the beginning of MIS 5a, a climate similar to present, but with higher rainfall, as
893 implied by the significant representation of deciduous oaks in the charcoal record and
894 the Mula, rather than the Mediterranean *rambla* it is today (dry for most of the year and
895 subject to torrential flash-floods in early autumn), then being a permanent stream along
896 whose margins boggy or lacustrine conditions persisted year-round.

897 • In the second half of MIS 5a, a progressive cooling of the climate, reflected in the
898 disappearance of *P. halepensis* from the charcoal record and the dominance of
899 *P. sylvestris/nigra* in both the pollen and the charcoal records.

900 • At the very end of MIS 5a and during the middle of MIS 3, a similarly cooler but more arid
901 climate, as implied by a juniper-dominated charcoal assemblage with rare cryophilous
902 pines and riverside trees; given the present distribution of *P. sylvestris/nigra* in the region
903 (above 1000-1200 m asl) and that the slopes surrounding Cueva Antón rise to no more
904 than 500-700 m asl, this implies bioclimatic belts lowered by at least 500 m, i.e.,
905 minimally, a 5 °C decrease in mean annual temperature.

906 This reconstruction is consistent with global records of climate change. For the GIs that
907 came after Heinrich Event 4, Fletcher et al. (2010) showed a recovery of trees in Europe
908 south of 40°N, matched in our record by the presence in semi-arid SE Spain of

909 *P. sylvestris/nigra* charcoal at 400 m asl during the formation of AS1. For the MIS 5a-to-
910 MIS 4 transition, Sánchez-Goñi et al. (2008, 2013) found a steady decrease in temperate
911 forest pollen from 82 to 72 ka in a marine core off the SW Iberian coast — matched in our
912 record by the rapid change from a *P. halepensis*-dominated charcoal assemblage in most of
913 AS5 to *P. sylvestris/nigra* -dominated pollen and charcoal assemblages in AS3 and AS2.
914 In Iberia, the terrestrial evidence for the periods of the Upper Pleistocene represented at
915 Cueva Antón remains scarce. Cueva del Camino (Arsuaga et al., 2012; Blain et al., 2014) and
916 Lezetxiki (Falguères et al., 2005) date to MIS 5 but, given their geographical location (in the
917 northern Meseta at 1114 m asl, and the Basque Country, in the bioclimatic Eurosiberian
918 region, respectively), are unrepresentative of the conditions that would have existed in the
919 Mediterranean. The Cova del Rinoceront, just south of Barcelona, features a long record
920 spanning MIS 6 and MIS 5 (Daura et al., 2015); its well-defined "tortoise horizon" could
921 represent MIS 5e, but the overlying sequence lacks the resolution required for correlation
922 with global records. By contrast, even though partial and limited in terms of the time span
923 covered, the Cueva Antón sequence provides "photographic" glimpses that add local detail
924 to the general picture derived from continuous, long-term sequences.
925 In other caves and rock-shelter sites of Iberia, the temperate and climatically transitional
926 intervals of the Upper Pleistocene tend to be lacking or form low-quality records. This
927 representativeness problem relates to the expansion of woodlands, which makes for
928 limestone country to be less frequented (if not abandoned) by humans, or for a thick
929 vegetation cover, with attendant soil stabilization, to imply depositional hiatuses and the
930 exposure of sedimentary fills to erosion, reworking and palimpsesting. Cueva Antón is

exceptional due to the fluvial nature of the sequence, which explains its thick, well-preserved and datable deposits, unique in their degree of stratigraphic integrity.

This sequence thus sheds light on why the climatically milder periods of the Middle and the Upper Paleolithic are so poorly represented, if at all, in the archeological record of the Iberian Peninsula. It has been debated whether such an absence could reflect actual human demography, or even extinction events (e.g., Bradtmöller, 2012; Galvan et al.; 2014, Garralda et al., 2014). Cueva Antón makes the point that the real problem lies in that we have been excessively dependent on the karst archive and need to be looking elsewhere.

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FIGURE CAPTIONS

Fig. 1. Cueva Antón: geographical setting. A. Location of the Middle Paleolithic sites of Murcia in a physical map of the region (after Zilhão and Villaverde, 2008; elevations in m asl). **B.** The mouth of the cave seen from the NE at the time of the 1991 salvage work (photo: C. Martínez-Sánchez). **C.** The cave seen from the NW on September 26, 2011, when the reservoir had dried out in front of the site. **D.** The site, the meander made by the Mula to enter the El Corcovado gorge, and the tectonic escarpments structuring the local landscape, overviewed from the NE on September 24, 2007. **E.** The mouth of the cave on September 19, 2009; the high water level prevented access to the site by land until the end of the following summer.

Fig. 2. Cueva Antón: the site. Top. Plan and grid. **Middle.** Schematic cross-section along the interface between rows 19 and 20 of the grid (DD = Dam Deposits; AS = Archaeological Succession; FP = Fine Palustrine). **Bottom left.** The East trench on September 7, 2011; the stratigraphic labels indicate the units exposed at this stage; on the foreground, note the 1 m² "telephone booth" (square I20), whose sediment was floated in its entirety. **Bottom right.** The cave's interior overviewed from the East on September 15, 2012, at the end of the field season.

Fig. 3. Cueva Antón: the 2011 floatation work. Left: the sediment columns sampled, at the end of their excavation, on September 8, 2011. **Right:** orthorectified photomosaic of the 1 m-wide, East cross-section of the I20 column. Elevations are in m asl.

Fig. 4. Cueva Antón: the reference stratigraphic cross-section. Orthorectified photomosaic of the West wall of grid units L/16-21 (originally taken in 2007, completed in 2011 to include archeological horizons III-b/d and III-i/j). Elevations are in m asl.

Fig. 5. Cueva Antón: East cross-section of grid units J/17-19. Orthorectified photomosaic taken at the end of the 2008 field season. In this area, layers II-a, II-c and II-b wedged out in row 19, and layer II-d changed into a hard calcareous crust marking the interface with the truncated, sloping surface of underlying sub-complex AS2. "I-k/II-d" is the designation given to the ensemble of AS1 layers, here archeologically excavated as a single unit. Elevations are in m asl.

Fig. 6. Cueva Antón: pollen percentage diagram. Stratigraphic variation across the L19 sampling column. The diagram was constructed using Tilia 1.12 and TiliaGraph v. 2.0.b.5. Ferns (*Filicales triletes*), Asteraceae (*Aster*-type, Cardueae, Cichorioideae) and other ubiquitous herbs with possible zoophily were excluded from the pollen sum.

Fig. 7. Cueva Antón: wood charcoal SEM microphotographs. **A.** I20-79 (II-y1): bacterial chain in *Quercus* sp. deciduous (x10,000). **B.** L19-54 (III-b/d): microorganism in *Juniperus* charcoal (x20,000). **C-D.** N21-3 (II-I): iron nodules within the tracheid of *Pinus* sp. (x5000) and detail of iron crystal (x18,000). **E-F**. L18[2006] (II-h/i): *Pinus sylvestris/nigra*, transversal (x100) and radial (x1000). **G-H.** K19-138 (III-i/j2): *Pinus halepensis*, transversal (x100) and radial (x1000).

Fig. 8. Cueva Antón: charcoal percentage diagram. Relative frequency of each ecological category in the studied fraction of each AS sub-complex (the Varia group has been excluded from the totals).

Fig. 9. Cueva Antón: the studied rabbit assemblages. Top. Age profiles. **Bottom.** Skeletal part representation (%NISP, after Dodson and Wexlar, 1979; Sk, skull; Mx, maxilla; Ud, upper dentition; Hem, mandible; Ld, lower dentition; Sc, scapula; H, humerus; R, radius; U, ulna; Cp, carpal bones; Mc, metacarpal; Cv, cervical vertebrae; Tv, thoracic vertebrae; Lv, lumbar vertebrae; Sv, sacral vertebrae; Cdv, caudal vertebrae; Rb, ribs; P, pelvis; F, femur; T, tibia; Ca, calcaneus; As, astragalus; Ta, tarsal bones; Pa, patella; Mt, metatarsal; Ph, phalanges; Se, sesamoid).

Fig. 10. Cueva Antón: rabbit bone taphonomy. Top. 1. beak punctures on medial side of ischion; 2. beak puncture on lateral side of a distal femur; 3-4. longitudinal fragments of tibial diaphyses with notched edges; 5-7. digested distal femora. Scale bars = 5 mm.

Fig. 11. Cueva Antón: larger mammal and tortoise taxonomy. 1-2. rhinoceros, upper and lower deciduous molars; 3. bear, lower premolar; 4. infantile deer, mandible with deciduous premolars; 5. red deer, lower third molar; 6. ibex, upper third molar; 7-8. Mediterranean tortoise, peripheral and costal carapace bones; 9-10. horse, incisor and lower molar; 11. roe deer, mandible with deciduous dentition; 12-13. foetal bones, proximal epiphysis of humerus and scapula; 14. deer, scapula. Scale bars = 1 cm.

Fig. 12. Cueva Antón: cut-marked bone from the 1991 salvage work. Detail of femoral shaft fragment of ibex-size mammal from layer III-i/j. Photo: José Paulo Ruas.

Fig. 13. Cueva Antón: piece-plotted items from the 1991 salvage work. Three-dimensional projection (elevation x5) over the south wall of the Zone I trench (squares J-

L22>23) after reclassification of the provenience information in Martínez-Sánchez (1997) to the occupation horizons defined in 2007-12. The scatter diagram displays clustering into the same, slightly NW-dipping lenses — layers III-b/d and III-i/j, separated by the thick, sterile cross-bedded sands making-up layer III-e/h —encountered when extending the 1991 trench to the North.

Fig. 14. Cueva Antón: hearths. Top left. Overview of the Extension trench (2012 field season) during excavation. **Top right.** Oblique view over the excavation of stratigraphic unit III-i/j1 as hearth features were being exposed in grid units N-O/19; the internal microstratigraphy of Hearth 4 is seen in the "pie-slice" trench excavated down to the base of the thermo-altered sands. **Bottom.** Base of the M-O19>20 stratigraphic cross-section; note the cross-bedding of the thermo-altered sands under both hearths and that Hearth 5 burned the lens of cross-bedded sands covering Hearth 4.

Fig. 15. Cueva Antón: stone tools from stratigraphic unit III-i/j3. A. O18-85, flint sidescraper; **B.** O18-102, flint sidescraper; **C.** N18-53, limestone core. Scale bars = 1 cm.

Fig. 16. Cueva Antón: correlation of the sequence with the global record. Charcoal percentage variation compared with the Greenland ice core oxygen isotope stratigraphy as well as with the variation in sea surface temperature and Mediterranean pollen observed across the 90-30 ka interval in a marine core off the Portuguese coast (Sánchez-Goñi et al., 2008, 2013; Rasmussen et al., 2014); the charcoal category with the highest frequency is indicated. Aligning the paleosoil formation at the top of sub-complex AS5 with the Greenland Interstadials falling within the interval indicated by OSL dating allows three correlation models. Model C best fits the signal detected in the site's paleoclimatic proxies.

1267 **TABLES**

1268 **Table 1. Cueva Antón stratigraphy.** Depositional environments recorded in the succession.

1269 The solid lines indicate major erosive surfaces, the dotted lines indicate minor

1270 discontinuities

Complex	Unit(s)	Depositional environment
DD		twentieth century artificial reservoir
TL		exposed surface
AS1	I-g, I-h, I-k	alluvial (floodplain plus bar/levee intercalation and one lacustrine event) alternating to (and ending with) wall degradation and runoff
	I-i	
	I-j, II-a	
	II-c	
	II-b	
AS2	II-d, II-e	alluvial bar/levee alternating to wall degradation and runoff
	II-f	
	II-g	fining upward alluvial sequence (channel, bar and floodplain), with intercalated events of wall degradation
	II-h, II-i	
	II-k	
	II-l top	
	II-l, II-m	
AS3	II- ñ, II-z, II-o	fining upward alluvial sequence (bar and floodplain) capped by lacustrine event
	II-p	wall degradation followed by alluvial floodplain
	II-q	alluvial sequence (channel, bar and floodplain) followed by wall degradation
	II-s	
	II-t	
AS4	II-ø	alluvial bar/levee
AS5	II-u	alluvial bar/levee with events of wall degradation and slope outwash
	II-w	
	II-t, II-y	
	III-a	
	III-b, III-c	alluvial bar/levee
	III-d	alluvial bar
	III-e, III-f, III-g	
	III-i	wall degradation and alluvial bar
	III-j	
	III-k	
	III-l	
	III-m, III-n	alluvial bar
FP	IV	'lacustrine'

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Table 2. Cueva Antón chronology. The dated radiocarbon samples. The ages have been calibrated against IntCal13 (Reimer et al. 2013) in Calib 7.0.4 (Stuiver and Reimer 1993); the calibrated ages are given as 95.4% probability intervals

Sample	Taxon	Field unit	Layer	Method	OxA	$\delta^{13}C$	Yield (mg)	% Yld	%C	Age BP	Age cal BP
E20-1	*Pinus halepensis*	dec 3	DD	ABOx-SC	20115	-22.5	12.07	12.6	75.4	98±23	–
K19-5	*Pinus nigra*	I-k/II-d	I-k	ABA	20882	-23.4	5.1	13.8	61.3	31070±170	34603-35360
I20-3	Conifer	I-k	I-k top	ABOx-SC	26346	-22.3	4.7	4.1	66.9	31790±270	35067-36245
G21-4	*Juniperus* sp.	dec 4	I-k base	ABOx-SC	22625	-21	8.6*	8.7*	77.9	32330±250	35627-36826
E21-11	*Juniperus* sp.	dec 5a	II-a	ABOx-SC	22019	-22.7	6.43	6	75.6	32390±280	35594-37055
J19-7	*Pinus* sp.	I-k/II-d	II-b	ABA	20881	-24	8.83	26.9	63.4	31150±170	34664-35446
				ABOx-SC	21244	-22.3	11.7*	12.1*	88.4	32890±200	36314-37714
N20-2	*Juniperus* sp.	II (4)	II-h/i	ABA	18672	-22.3	5.7	21.1	60.1	39650±550	42551-44355

*These values are estimated as only approximately half of the sample remaining after the wet chemistry was pre-combusted.

Table 3. Cueva Antón luminescence dating. Variation of Burow et al.'s (2015) quartz OSL dates (MG = multiple grain; SG = single grain; see also SI Table 1), based on a long-term WC (water content) of 5%, as a function of variation in this parameter; sample elevation has been rounded to the nearest 5 cm fraction

Stratigraphic unit	Lab code and sample field number	Cross-section and elevation (m asl)	Sample's measured WC (%)	Method	Age (ka)			
					WC=2.5%	WC=5%	WC=12%	WC=20%
2010 samples								
AS2, II-e	C-L2941, CA-1	J19 East, 354.45	18.9	MG	69.1±7.1	70.9±7.6	75.8±8.4	81.3±9.3
				SG	71.1±7.2	72.9±7.7	78.0±8.5	83.6±9.4
	C-L3137, CA-2	J19 East, 354.35	4.1	MG	67.6±7.2	69.3±7.7	74.3±8.4	79.8±9.3
AS5, II-y	C-L2942, CA-4	J20 East, 353.20	16.7	MG	67.6±6.7	69.4±7.2	74.6±8.0	80.4±8.9
AS5, III-f	C-L2943, CA-5	J20 East, 352.85	8.4	MG	68.1±7.1	69.9±7.6	74.9±8.4	80.5±9.3
				SG	66.9±6.4	68.7±6.8	73.6±7.6	80.1±8.1
AS5, III-m	C-L3138, CA-6	L21 West, 352.20	12.3	MG	75.4±9.2	77.5±9.8	83.3±10.6	89.8±11.7
2012 samples								
AS4, II-ø	C-L3375, CA-9	L21 West, 353.20	1.5	MG	80.1±7.4	82.2±8.0	88.2±8.9	94.9±9.9
AS5, III-e/h	C-L3376, CA-10	L21 West, 352.70	1.9	MG	70.3±7.3	72.2±7.8	77.4±8.6	83.2±9.6
AS5, III-k/l	C-L3377, CA-11	L21 West, 352.45	2.3	MG	72.2±7.4	74.1±7.9	79.5±8.8	85.7±9.7
AS5, III-m	C-L3378, CA-12	L20 West, 352.25	3.3	MG	67.2±6.9	69.1±7.3	74.2±8.1	80.1±8.9

Table 4. Cueva Antón mollusks. Assemblage composition by ecological category and depositional environment

					Species habitat preference					
Layer(s)	Complex	Context	TOTAL	Obs.	Catholic	Scree	Dry	Marsh	Aquatic	Other
I-k	AS1	temporarily inundated slope deposit	1002	(a)	265	9	92	518	117	1
II-a to II-b	AS1	floodplain, bar/levee, lacustrine	54	(b)	15	2	7	12	17	1
II-d to II-f	AS2	bar/levee	1	(c)	–	–	–	1	–	–
II-g to II-i	AS2	channel, bar, floodplain	–	(d)	–	–	–	–	–	–
II-k	AS2	bar *cum* slope deposit	3	(e)	1	–	–	–	2	–
II-l & II-m	AS2	channel, bar	3	(f)	2	–	–	–	–	1
II-ñ to II-o	AS3	channel, bar, lacustrine	18	(g)	4	–	4	4	5	1
II-p	AS3	floodplain	177	(h)	57	–	52	56	12	–
II-q to II-t	AS3	channel, bar, floodplain	4	(i)	1	2	–	–	1	–
II-u	AS5	bar, levee, paleosoil	401	(j)	111	2	115	61	112	–
II-y to III-n	AS5	bar	152	(l)	17	–	96	14	22	3
IV (upper)	FP	lacustrine	70	(l)	1	25	17	20	6	1

(a) of four sediment samples, all yielded shell
(b) of eight sediment samples, all yielded shell
(c) of five sediment samples, only one yielded shell
(d) of nine sediment samples, none yielded shell
(e) of three samples, one opened during transport and most of the contents had emptied; another yielded no shell
(f) of eight sediment samples, three yielded shell
(g) of seven sediment samples, only three yielded shell, of which one opened during transport and most of the contents had emptied
(h) of two sediment samples, both yielded shell
(i) of ten sediment samples, only one yielded shell
(j) of four sediment samples, all yielded shell
(k) of 23 sediment samples, 16 yielded shell, of which three opened during transport and most of the contents had emptied
(l) from one sediment sample only

Table 5. Cueva Antón larger mammals and tortoise. Stratigraphic distribution per taxon (or body size, for undetermined specimens)

	I-k/II-d		II-k/II-m		II-p/q/t		II-u		II-y		III-b/d		III-i/j		TOTAL	
	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
Artiodactyla																
Roe deer	–	–	–	–	–	–	–	–	–	–	1	1	2	2	**3**	**3**
Deer	2	1	2	1	1	1	11	1	2	1	70	4	86	11	**174**	**20**
Ibex	–	–	–	–	–	–	–	–	–	–	9	3	13	4	**22**	**7**
Foetus/neonate	–	–	–	–	–	–	1	1	–	–	11	3	3	2	**15**	**6**
Perissodactyla																
Horse	–	–	5	1	1	1	–	–	–	–	5	2	9	4	**20**	**8**
Rhino	–	–	–	–	–	–	–	–	–	–	–	–	10	1	**10**	**1**
Carnivora																
Bear	–	–	–	–	–	–	–	–	–	–	–	–	1	1	**1**	**1**
Testudines																
Tortoise	–	–	–	–	–	–	–	–	–	–	12	2	28	4	**40**	**6**
Ungulates per body size																
Small	13	–	3	–	1	–	4	–	4	–	34	–	46	–	**105**	–
Medium	18	–	17	–	2	–	10	–	6	–	85	–	212	–	**350**	**–**
Large	1	–	–	–	–	–	–	–	–	–	4	–	20	–	**25**	–
TOTAL	**34**	**1**	**27**	**2**	**5**	**2**	**26**	**2**	**12**	**1**	**231**	**15**	**430**	**29**	**765**	**52**

Table 6. Cueva Antón stone tools. Stratigraphic distribution per raw-material and technological category of piece-plotted items from the 1991 and 2007-12 field seasons. For each unit, the approximate area (in m^2) of the excavated surface is indicated between brackets

		I-k [54]	II-c [54]	II-k [35]	II-l [35]	II-m [35]	II-q/t [26]	II-u [26]	II-y [25]	III-b/d [25]	III-e/h [25]	III-i/j [25]	III-m [3]
Flint	Cores	2	–	–	3	–	–	–	–	7	–	8	–
	Debitage	7	–	–	5	–	–	3	–	61	1	137	–
	Tools	3	–	–	7	1	–	1	–	30	1	56	–
	Debris	7	–	2	8	–	–	–	2	21	2	63	1
	Total	19	–	2	23	–	–	4	2	119	4	264	1
Limestone	Cores	–	–	–	1	–	–	–	1	11	–	9	–
	Debitage	–	–	–	5	–	1	–	–	141	–	50	–
	Tools	–	–	–	1	–	–	–	–	13	–	6	–
	Debris	–	1	–	–	–	–	–	–	56	–	17	–
	Total	–	1	–	7	–	1	–	1	221	–	82	–
Quartzite	Cores	–	–	–	–	–	–	–	–	1	–	–	–
	Debitage	–	–	–	–	–	–	–	–	3	–	8	–
	Tools	–	–	–	–	–	–	–	–	–	–	–	–
	Debris	–	–	–	–	–	–	–	–	–	–	1	–
	Total	–	–	–	–	–	–	–	–	4	–	9	–
TOTAL		**19**	**1**	**2**	**30**	**1**	**1**	**4**	**3**	**344**	**4**	**355**	**1**